

The Biology of Paternal Care in Human and Nonhuman Primates

Eduardo Fernandez-Duque,^{1,2} Claudia R. Valeggia,^{1,2} and Sally P. Mendoza³

¹Department of Anthropology, University of Pennsylvania, Philadelphia, Pennsylvania 19104; email: eduardof@sas.upenn.edu, valeggia@sas.upenn.edu

²Centro de Ecología Aplicada del Litoral-Conicet, Corrientes 3400, Argentina

³California National Primate Research Center, University of California, Davis, California 95616; email: spmendoza@ucdavis.edu

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Abstract

Among primates, intense paternal care is manifested in only a few distantly related species, including humans. Thus, neither purely phylogenetic nor socioecological hypotheses can explain its presence or the variability in the expression of paternal behaviors. Traditional theoretical models for the evolution of paternal care can now be reexamined, focusing on male–female interactions as a possible key to understanding parental strategies. At a proximate level, the existing evidence implies a common physiological substrate for both paternal behavior and pair-bonds. Vasopressin, and perhaps prolactin and testosterone, apparently underlies the endocrinological bases of paternal care, and neuroanatomical reward pathways may be involved in the formation of attachment bonds. Understanding of the genetic structure of primate populations and the neurogenetics of social behavior is also emerging. A multidisciplinary approach that also considers epigenetic and transgenerational effects promises to open new avenues to explain the flexible nature of paternal care in primates.

Paternal care:

behaviors performed by putative/social fathers, which appear to have positive effects on infant development, growth, well-being, and/or survival

Paternal investment:

behaviors performed by putative/social fathers, which increase the probability of the infant's survival

INTRODUCTION

Few aspects of primate behavior are so intriguing, yet so poorly understood, as the expression of intense paternal care. Although rare, paternal care in a few primate species and some human societies includes providing protection from predators and other conspecifics, sharing food, playing, grooming, carrying infants, teaching hunting skills, and singing lullabies. All avian and mammalian males face the uncertainty of paternity because of internal fertilization. Participation of mammalian fathers in the most essential parental activities is further constrained by pregnancy and lactation. Yet, in spite of these limitations, some primate males display intense paternal care (Gubernick & Klopfer 1981, Kleiman 1985, Kleiman & Malcolm 1981, Smuts & Gubernick 1992, Whitten 1987, Wright 1990).

Field and laboratory data on primate paternal care have accumulated to the point where a synthesis of its expression is possible. Paternal care among primates, illustrated in its extreme form by our research on a few nonhuman primate species and some human societies, is varied (Di Fiore et al. 2007; Fernandez-Duque et al. 2008, 2009; Mendoza & Mason 1986a,b; Rotundo et al. 2005; Valeggia 2009; Wolovich et al. 2008). Using information from disciplines as disparate as evolutionary biology and neuroscience, we provide an initial attempt to understand this variation, ecological and social determinants, and common proximate mechanisms.

A TAXONOMY OF PATERNAL CARE

Paternal Care and Paternal Investment

Paternal/parental care, biparental care, paternal/parental investment, and alloparental care are terms regularly mentioned in the primate literature. Given the different ways in which they are used, it is important to state that our work has focused on paternal care, not paternal investment. Paternal care and paternal investment are frequently used interchangeably, and wrongly so (Sheldon 2002). Thus, we do not

attempt to relate the two terms or to use paternal care as proxy for paternal investment.

Paternal care is a suite of behaviors performed by a mature male (the putative/social father of the immature young), which would not be performed in the absence of the young. These behaviors are directed to the infant and have a positive effect on infant development, growth, well-being, or survival. They may include carrying, grooming, playing, sharing food, feeding, cleaning, retrieving, huddling, babysitting, defending, and teaching. Some of these behaviors may continue beyond the stage of development when they are necessary for infant survival. This is so because infant primates, unlike other mammals, experience a long period of dependency during which they require significant assistance.

Infants play an active role in directing their own development and have considerable skill in eliciting care behaviors. Generally the mother is the primary target of the infant's solicitation of care, but in many primate species other group members are also responsive to infants. Alloparental care, care provided by nonmothers, has received significant attention recently (Hrdy 2005, 2008; Ross & MacLarnon 2000; Tardif 1997), but here we are concerned with the relatively rare situation where alloparental care is provided by the putative father.

Paternal care, as defined above, is widespread among birds and fish and is occasionally present in amphibians, insects, and worms (Beltran & Boissier 2008, Clutton-Brock 1991, Trumbo 2006, Zeh & Smith 1985). On the other hand, paternal care is relatively rare in mammals. Among the mammalian orders, it is more frequent in carnivores, rodents, and primates (Kleiman & Malcolm 1981, Woodroffe & Vincent 1994).

Paternal Care in Nonhuman Primates

In most primates, males may be tolerant of infants, or they may occasionally interact affiliatively with them without any clear direct or indirect paternal care provided (Whitten 1987, Wright 1990). The most conclusive evidence

for the benefits that infants may accrue from these infrequent interactions with males comes from studies of wild savannah baboons (*Papio cynocephalus*). Adult males selectively support their offspring in agonistic disputes with a direct effect on the offspring fitness (Buchan et al. 2003, Charpentier et al. 2008). It is still not fully understood whether fathers can somehow recognize offspring likely to be their own or if it is a generalized response to all infants. Still, the putative father interacts affiliatively with infants only in very particular and restrictive circumstances.

It is only among a handful of primate genera that the relationship between males and infants takes on a qualitatively different form. Among siamangs, tamarins, marmosets, titi monkeys, owl monkeys, and some human societies, paternal care is direct, conspicuous, and sustained across time and circumstance. These taxa are only distantly related, suggesting that paternal care may result from evolutionary trajectories developing under different social and ecological conditions (**Figure 1**; Di Fiore & Fernandez-Duque 2007).

Paternal care among siamangs is intriguing. All hylobatids (i.e., gibbons, lesser apes) show the traditional correlates of paternal care—social monogamy, territoriality, and reduced sexual dimorphism—but it is only the siamangs (*Symphalangus syndactylus*) that show paternal care. Female siamangs take exclusive care of the infants during the first year of life, but adult males and older juveniles carry infants beginning in the second year (Chivers 1974, Lappan 2008).

Generalized sharing of infant transport is also exhibited by the callitrichids of South America (**Figure 1**). Alloparental care (also called cooperative breeding) is the norm, and the mother, father, siblings, and other group members share in the care of the twins (or triplets) that are born twice a year (Bales et al. 2000, Tardif et al. 2002, Tardif & Garber 1994, Zahed et al. 2007, Ziegler 2000). The infants appear to be highly attractive to group members who often compete for the opportunity to carry dependent infants.

Nowhere is paternal care more extensive and more obligate than among titi monkeys (*Callicebus*) and owl monkeys (*Aotus*, **Figures 2** and **3**). Both genera live in small groups consisting of an adult pair and 2–4 young (Fernandez-Duque 2007, Norconk 2007). Females give birth to a single infant each year and the male is the primary carrier for the infant, each assuming their roles soon after birth. Dependent infants may be carried as much as 90% of the time by their putative fathers and transfer to the mother for brief periods usually surrounding active nursing bouts (Dixon & Fleming 1981, Fernandez-Duque et al. 2009, Fragaszy et al. 1982, Mendoza & Mason 1986b, Wright 1984). Siblings very infrequently participate in transport of the infant (Fernandez-Duque et al. 2008). In titi monkeys, infants develop a preference for their fathers over their mothers (Mendoza & Mason 1986b), demonstrated via a strong pituitary-adrenal stress response when separated from their fathers but not from their mothers (Hoffman et al. 1995).

Paternal Care in Human Societies

Human societies vary in the expression of paternal care, from complete absence or aloofness to great intimacy and direct care. A range of variation manifested even within foraging societies. At one end, Aché fathers of the Paraguayan forests seldom hold or interact with infants and young children (Hill & Hurtado 1996). At the other end, male Aka Pygmies are heavily involved in paternal care, spending up to 22% of their time holding young infants (Hewlett 1991).

Societies in both developed and developing countries, with varying levels of industrialization fall within this broad spectrum of expression of paternal care. Intercultural variability in fathering seems to be associated with the local ecology and social environment. Household composition, availability of mating opportunities and resources, the extent of extrinsic mortality, and pathogen stress have all been identified as potential correlates of paternal care in

Alloparental care/Cooperative breeding: infant and young care provided by individuals other than the mother

Attachment: an enduring form of emotional bond between two individuals

humans (Hewlett 1991, 1992; Marlowe 1999; Quinlan 2007).

In addition to the great variability in paternal care among human groups, there is usually significant variation among men within societies known for their high levels of paternal care. In those societies, some men do not participate in child care, whereas others cannot do more (Hewlett 1991). Even though human mothers clearly need a considerable amount of help rearing their offspring, paternal care among humans is highly variable and far from a universal trait. This disconnect leads anthropologist Sarah Hrdy to talk about “the paradox of facultative fathering” in the human species (Hrdy 2005, 2008).

EVOLUTION OF PATERNAL CARE

The 1970s and 1980s brought a series of predominantly qualitative theoretical models that attempted to explain the evolution of parental investment or parental care (Dawkins & Carlisle 1976, Hamilton 1984, Kurland & Gualin 1984, Lancaster & Lancaster 1983, Maynard Smith 1977, Trivers 1972). The models emphasized primarily parental investment with a focus on cost-benefit analyses. Nonetheless, two hypotheses remain particularly relevant in attempting to explain the evolution of paternal care.

The first hypothesis is that paternal care evolved in response to the necessity of obligate biparental care to rear offspring successfully (Achenbach & Snowdon 2002; Fite et al. 2005; Hill & Hurtado 1996; Key & Aiello 2000; Miller et al. 2006; Smucny et al. 2004; Tardif 1997; Tardif et al. 2005; Van Schaik & Kappeler 1997; Wright 1984, 1990; Ziegler et al. 2006). This hypothesis seems particularly relevant for explaining the evolution of alloparental care in the callitrichids. The mother, whose body mass is often exceeded by the combined body mass of her infants is incapable of raising the offspring on her own and even a male-female pair have difficulty raising

twins successfully. Her situation is further compounded by a postpartum estrous that results in females being simultaneously and continuously pregnant and lactating. Most callitrichids have elaborate behavioral and physiological mechanisms that prevent nondominant group members from participating in reproduction and thereby facilitate paternity certainty. The care provided by the male (or other conspecifics) contributes to reducing the metabolic costs to the female of raising the offspring as illustrated by the fact that callitrichid males lose weight when they are providing most infant transport. The obligate biparental care hypothesis has less appeal for other species exhibiting intense paternal care, such as titi and owl monkeys.

The second hypothesis considers the affiliative interactions between males and infants as a mating strategy by males that helps them develop a relationship with a female and secure a position in the larger social network. The hypothesis has been useful to examine male-infant interactions in taxa where there is no conspicuous and direct care (Smuts & Gubernick 1992), and more recently in humans (Marlowe 2000). The relationship between paternal care and the development of emotional attachments (or pair-bonds) in humans has played a central role in evolutionary models of human behavior (Geary & Flinn 2001, Hawkes 2004; see sidebar, Attachment Bonds). Investigators have historically argued that pair-bonds evolved given the female need for paternal infant care and provisioning. For example, men in Xhosa (South Africa) invested the most (in terms of money and time) in their coresiding putatively biological children and the least in the step-offspring of a former partner (Anderson et al. 1999, 2007). However, biological children living with a former partner and stepchildren of current partners receive similar levels of investment. Among the Hazda of Tanzania, biological children receive more care (both direct and indirect) than do stepchildren (Marlowe 1999). Thus men provide care to their partner's offspring as a component of their mating

strategy, but they tend to provide more to their own offspring. This tendency suggests that paternity confidence plays an important role in shaping men's relationships with women and with their putative genetic children (Anderson 2006). These studies illustrate problems inherent in quantifying and differentiating parental investment and parental care. This is true particularly when men may be providing investment or care for children that will have benefits only in the very long term (e.g., college tuition, teaching hunting skills).

These early models were extremely influential and shaped the research on paternal care and parental investment during the next decades. Their impressive contributions notwithstanding, it cannot be overemphasized that they were developed and evaluated on very limited data. Bateman's and Trivers' contributions have recently been reexamined with some fascinating new insights (Parker & Schwagmeyer 2005, Queller 1997, Wade & Shuster 2002). Wade & Shuster (2002, p. 291) proposed that "differences in initial parental investment between the sexes are likely to arise from rather than lead to sexual selection favoring increased mate numbers in males and emphasis on parental care by females." This effectively reverses the direction of causality between sexual selection and parental investment and would lead, if accepted, to a major reconsideration of sex differences in parental care (Kokko & Jennions 2003). Other authors continue to remind us of the need to abandon the now untenable traditional view of coy females and ardent males championed by Bateman and Trivers and followed dogmatically ever since (Snyder & Gowaty 2007, Tang-Martinez & Ryder 2005). We have enough evidence in a wide range of taxa, primates included, to show that the relative contributions of males and females in the shaping of social systems and in the provision of care are better understood as the outcome of a conflict between the sexes. A conflict during which females regularly exercise choice and control and during which female promiscuity is far from an exception (Gowaty 1996, 2004; Hrdy 2000).

ATTACHMENT BONDS

In many species, infants are highly motivated to form an emotional bond with their mothers (Bowlby 1969) and, in the absence of the mother, will direct filial attachment to the closest individual (Mason & Kenney 1974). Ainsworth (1969) elaborated the elements of attachment bonds to include the following: (a) individual recognition, (b) specific preference, and (c) separation distress (Mendoza et al. 1980). Infant monkeys will return to their attachment figure when distressed, suggesting that stress-buffering or secure base is also a component of attachment (Suomi 1999). Using these criteria it is possible to determine whether affiliative relationships qualify as attachment or something more akin to friendship (Mendoza et al. 1991). In titi monkeys, infants form a unidirectional attachment bond with their fathers, which persists into adulthood; mothers are less effective attachment figures in the absence of the father (Hoffman et al. 1995, Mendoza & Mason 1986b). Mothers and fathers do form attachment bonds with each other, but not with their offspring. Other nonattachment relationships among family members are amicable (including close following, play, food sharing, and passive contact). Thus it is not possible to distinguish attachment bonds on the basis of proximity or contact alone, as has been often incorrectly assumed.

ENDOCRINE, GENETIC, AND NEURAL SUBSTRATES OF PATERNAL CARE

Hormonal Substrates of Paternal Behavior

The hormonal correlates of paternal care in mammals have not been as extensively studied as those of maternal care (Bridges 2008). In females, mechanisms regulating maternal behavior may be derived from processes involved in birth or, for mammals, in the regulation of lactation. Sudden changes in progesterone, estrogen, oxytocin, and prolactin, all involved in birth or lactation, are also implicated in maternal behavior. Therefore, although it is reasonable to suppose there is overlap between mechanisms supporting maternal and paternal behavior, it is unlikely that they are the same ones related to birth and lactation, which obviously do not have male parallels. When

examining the hormonal basis of paternal care, we are compelled to signal the correlational nature of most of the evidence and the bidirectionality of hormone-behavior interactions (Almond et al. 2008, Schradin & Anzenberger 2002).

Prolactin, a peptide secreted by the anterior pituitary gland, has long been associated with maternal care in birds and mammals (Ziegler 2000). Prolactin also appears to be involved in paternal care in a variety of species (Schradin & Anzenberger 1999, Wynne-Edwards & Timonin 2007, Ziegler 2000). Among some of the neotropical primates that display intense paternal behavior, adult reproductive males show changes in prolactin levels associated with fatherhood (Schradin et al. 2003). The way prolactin changes are associated with paternal care widely varies, and this variation could reflect the different ways in which males experience and express infant care. In humans, the role of prolactin in paternal care is not straightforward. Parental experience affects men's prolactin responses, but recent contact with infants and individual differences in responses to infant cues may be responsible for the hormonal changes rather than the reverse (Delahunty et al. 2007, Fleming et al. 2002, Gray et al. 2007). No evidence as yet indicates that elevations in prolactin actually contribute to the expression of paternal behavior. Because prolactin is stress responsive and is regulated by each of the monoamine systems involved in emotion regulation, the prolactin changes attendant to interactions with the infant may be epiphenomenal.

Investigators have conclusively associated two other peptide hormones, oxytocin and vasopressin, with parental care. Oxytocin is implicated in maternal behavior and in female reproduction through its role in parturition, milk let down during lactation, sexual behavior, and sperm transport (Pedersen et al. 2006, Pedersen & Prange 1985). Although oxytocin may underlie the expression of paternal behaviors (Parker & Lee 2001), contradicting evidence indicates otherwise (Bales et al. 2004a). Vasopressin has been implicated in other sociosexual behaviors

including courtship, male-male competition, and pair-bonding (Lim et al. 2004a, Moore 1992). Both sexes respond to both peptides, but oxytocin seems to be more relevant in females and vasopressin in males (Bales et al. 2004b, Carter 2007, Carter et al. 2008b). The sexually dimorphic physiological and behavioral effects of oxytocin and vasopressin appear to be conserved in humans as well (Feldman et al. 2007, Gray et al. 2007, Sanchez et al. 2009).

Testosterone is a steroid hormone strongly associated to reproduction and infant care. One seminal idea in behavioral endocrinology is that testosterone is antagonistic to infant care, and males may have to make trade-offs between mating effort and parental care (Ketterson & Nolan 1999, Wingfield et al. 1990). For example, marmoset males who carried infants the most had the lowest urinary testosterone levels (Nunes et al. 2001) and the most significant declines in gonadal steroids (Nunes et al. 2000). Male titi monkeys do not show changes in gonadal steroids with the birth of infants, but changes in adrenal steroids suggest that the animals become more stress responsive with the advent of new infants (Reeder 2001). Among humans, several cross-cultural studies indicate that married men with young children tend to have lower testosterone levels than single, unpaired men and married men with no children (Berg & Wynne-Edwards 2001; Gray et al. 2006, 2007; Muller et al. 2008; Storey & Walsh 2000). Although the evidence is not wholly in line with the idea that testosterone is inimical to paternal behavior, the evidence is strong that steroid hormones are involved in expression of paternal behavior.

Genetic Substrates of Paternal Behavior

Genetic studies are making significant contributions in at least two aspects relevant to understanding paternal care. First, they provide data on the biological relatedness between care providers and infants. The presentation of these data will be a most crucial contribution because theoretical formulations have

generally assumed that care providers will adjust their investment on the basis of paternity certainty, which may not always be true (Queller 1997, Sheldon 2002). Second, they are helping us understand the neurogenetic basis of social behavior.

Paternal care and paternity. Molecular genetic studies, combined with long-term behavioral and demographic data, are required to determine biological relatedness and reproductive success. Most primate studies of genetic structure have focused on polygynous species (Altmann et al. 1996, Di Fiore & Fleischer 2005, Gagneux et al. 1999, Keane et al. 1997). Genetic evidence has been used to suggest that some males in polygynous species intervene in agonistic disputes or defend infants from infanticidal males in a manner that directly favors the development and/or survival of their offspring (Borries et al. 1999, Buchan et al. 2003, Charpentier et al. 2008). That said, even if it is shown that males are somehow intervening in favor of their offspring, the nature of their interventions are qualitatively different from those observed in taxa in which there is direct and conspicuous care. Thus, the genetic substrates of the neurobiological mechanisms underlying a tendency to interfere in agonistic disputes would be expected to be different from the ones underlying behaviors such as infant retrieval, transport, and active food sharing.

Unfortunately, only a handful of studies have examined genetic paternity among taxa with direct paternal care. In at least one marmoset species (*Callithrix kublii*), genetic chimerism, mixing of two or more genomic lineages within an individual, changes the predicted pattern of 50% sharing of genetic information in siblings (Ross et al. 2007). The caregivers could apparently detect differences due to chimerism inasmuch as males carried chimeric infants more often than nonchimeric ones. Among mustached tamarins and common marmosets, most infants were sired by one male, but nonfathers participated in carrying infants (Huck et al. 2005, Nievergelt et al. 2000). Among fat-tailed dwarf lemurs, there is a high rate of extrapair

paternity and social fathers provide care to extra-pair young (Fietz & Dausmann 2003, Fietz et al. 2000).

No published studies have yet described the genetic structure of populations of titis and owl monkeys in which paternal care is most intense. Still, on the basis of their dispersal patterns, serial monogamy, and mtDNA population structure (Babb et al. 2008, Bossuyt 2002, Fernandez-Duque 2009, Rodman & Bossuyt 2007), it seems likely that the potential genetic benefits of providing paternal care will need to be considered at a community level as has been suggested for gibbons (Reichard 2003). Relatively short dispersal distances and a fast rate of adult replacement may result in males providing care to young who are not their offspring but who are still closely related kin.

Genetics, pair-bonding, and paternal care.

Recent attempts to examine the genetics of pair-bonding and paternal care in primates are exciting, but correlational and preliminary. Thus far, they have focused on the potential role of the distribution and quantity of neural receptors for vasopressin (Donaldson & Young 2008, Walum et al. 2008). In voles, polymorphisms in the promoter region of vasopressin receptor 1a gene (*avpr1a*) apparently contribute to behavioral differences between monogamous and polygynous males by altering gene expression and ultimately the distribution and density of vasopressin receptors in brain tissue (Hammock & Young 2005). Primate mating and social behaviors may also be influenced by variation in the number of repeat sequences in the promoter region of the *avpr1a* gene (Rosso et al. 2008, Walum et al. 2008), but evidence on a large number of rodent species strongly indicates that it is extremely unlikely that similar mechanisms are regulating such complex behaviors in humans and nonhumans alike (Fink et al. 2007).

Neural Substrates of Paternal Behavior

At this point, we know very little about the neural substrates of primate paternal behavior. Because paternal behavior co-occurs with

Genetic chimerism:

a mixing within an individual of two or more populations of genetically distinct cells that originated in different zygotes

Extra-pair paternity:

a male sires an infant with an individual other than the pair-mate

Epigenetic effects:

heritable changes in gene expression or phenotype that occur without changes in the underlying genetic sequence

pair-bonding, we can use studies of pair-bonding to supplement what is known, and in doing so, we must draw heavily from studies of monogamous prairie voles (Nair & Young 2006). Two components of the neural circuitry underlie pair-bonding and paternal behavior in voles: a cognitive component required for individual recognition and an emotional component that provides the reward for engaging with particular other individuals (Lim et al. 2004b; Liu et al. 2001; Young et al. 2001, 2005). These circuits did not evolve specifically to support paternal behavior; rather they are an elaboration of existing social recognition and reward circuits that function in a variety of behaviors.

Titi monkeys seem to have neurobiological mechanisms of pair-bonding that parallel the pathways identified in voles. Male titi monkeys that were in long-term pair-bonds (conflating pair-bonding and paternal experiences) showed differences in glucose uptake when compared with males living alone (Bales et al. 2007). The lone males in that study were subsequently paired and PET scans repeated. Then, males in new pairs (without paternal experience) showed some changes in neural activity in the direction of males in long-term relationships but overall were not as different from lone males as they were from males in long-term bonds.

The neurobiological mechanisms facilitating pair-bonding and paternal care may be elaborations of mechanisms that foster sociality more generally. Familiar conspecifics attenuate behavioral and physiological stress in rodents and primates (Gust et al. 1994, Kiyokawa et al. 2004, Mendoza & Mason 1986a, Ruis et al. 1999, Terranova et al. 1999). The pathway by which the social environment influences stress responsiveness has been partially identified and is believed to include activation of oxytocin and vasopressin pathways and ultimately the dopamine and opiate reward pathways in the brain (Carter et al. 1999). Monogamous voles, as compared with nonmonogamous voles, have a greater density of oxytocin receptors in neural structures involved in the reward pathway. Male voles also have a much higher level of vasopressin receptors in structures necessary for

both reward and social cognition (Lim & Young 2006). The evidence in primates is still limited, but fatherhood apparently increases the abundance of vasopressin receptors in the brains of male marmosets (Kozorovitskiy et al. 2006). In humans, a recent review of studies using functional neuroimaging indicates that responses to infant stimuli include the same circuitry identified in rodent and nonhuman primate studies and thus are highly conserved through evolution (Swain et al. 2007).

DEVELOPMENTAL PROGRAMMING AND TRANSGENERATIONAL INFLUENCES

The studies reviewed above give strong support to hypotheses that involve certain neural and endocrine pathways in the expression of paternal care. However, evidence is accumulating that shows epigenetic effects on parental behavior and an increasingly important role of early experience in shaping its development (Carter et al. 2008a, Champagne & Meaney 2007, Michel & Tyler 2007). Laboratory experiments with prairie voles have shown that relatively subtle changes in early experience (e.g., handling of pups, licking, sniffing) have long-term consequences for later social behavior of the offspring. A single handling event in the postnatal period was associated with increased future paternal care in male offspring (Carter et al. 2008a). In turn, these differences in early experiences were correlated with changes in oxytocin and vasopressin patterns in adulthood. Variation in early experiences, then, could be translated into endocrine signals that would influence certain behavioral patterns later in life. For example, epigenetic influences on early oxytocin modulation may be implicated in social aspects of personality and may be the underlying base for some psychiatric disorders such as autism, anxiety, and depression (Carter 2007, Swain et al. 2007). Along the same lines, it is not unreasonable to expect that a stable environment during early development may modulate the establishment of neuroendocrine pathways

that would promote certain types of parental behaviors, on the basis of that early experience, which would be differentially expressed in the adult.

Evidence of developmental programming of social behavior via epigenetic effects introduces the possibility of transgenerational influences in the development and expression of paternal care. Hypotheses of developmental programming of parental behavior, stemming mostly from studies with biparental rodents (Michel & Tyler 2007), are receiving considerable attention. Systematic research in primates, however, is still scarce. Preliminary data from titi monkeys indicate that males with lesions to a very small part of the prefrontal cortex were more tolerant of other group members and hence spent even more time in contact with mates and offspring than is typical. The offspring of lesioned males, in turn, were more likely to engage affiliatively with their siblings (S.P. Mendoza, W.A. Mason, J. Padberg, and K. Bales, unpublished data). Significantly, these males showed more extreme differences in brain regions associated with social recognition and reward when compared with lone or newly paired males than did the nonlesioned males in long-term bonds (Bales et al. 2007). In humans, several hypotheses propose a relationship between childhood experiences and an adult focus on mating or parenting effort (Belsky et al. 1991, Chisholm 1993, Geary 2000, Quinlan 2007). According to these views, local unstable environments (e.g., high mortality risks, low resource availability) during childhood would be associated with a higher focus by men on mating rather than on parenting. This focus on mating would lead to less-responsive paternal behaviors. Although the existing evidence is scant, there may be developmental influences modulating the degree of paternal involvement.

CONCLUSIONS

Among primates, paternal care is present in a wide range of body sizes, from the small calitrichids (0.5–0.7 kg) to siamangs (5–7 kg) and humans (50–70 kg). Paternal care is present

with and without simultaneous sibling care. Sometimes, within the same genus, paternal care is present in extremely varied ecological settings. For example, the owl monkey species ranging evergreen tropical forests exhibit patterns of paternal care that are similar to the ones showed by owl monkeys in relatively dry subtropical forests. In some taxa, paternal care is omnipresent, whereas in others its frequency and intensity are more variable. It seems reasonable to conclude that paternal care has evolved independently at least a few times in the radiation of the primate order.

Long-term behavioral and demographic data strongly indicate that direct, conspicuous and frequent paternal care tends to occur simultaneously with the development of a pair-bond between the mother and the putative father providing care. An association between pair-bonds and paternal care is further supported by our understanding of the proximate mechanisms underlying these aspects of the social behavior of primates. There seems to be a common biological substrate with similar neuroanatomical and neuroendocrine processes regulating the manifestation of pair-bonds, monogamy, and paternal care. Following the lead of the rodent research, it is increasingly likely that neurobiological processes underlying paternal behavior are related to mechanisms that promote social behavior generally. Still, much more work is needed to identify the precise mechanisms that are altered to facilitate expression of paternal care. The most promising research is on vasopressin and its receptor quantity and distribution, which is closest to being linked to enhanced sociality. It is unlikely that vasopressin will fully explain the intriguing role that emotional bonds seem to play in the expression of the monogamous social system in titi monkeys, but it may act on them to facilitate expression of paternal care. We tend to think in human terms that something akin to love motivates fathers to provide care for their infants. This is not the case in titi monkeys in which the fathers are tolerant, nonrejecting, and nonaggressive to their infants but show no evidence of an emotional bond with them.

Perhaps, all that is needed to bring about the expression of paternal behavior is a relatively small change in mechanisms regulating social tolerance, rather than an elaborate mechanism specifically designed for that end. For example, vasopressin may be playing a prominent role in regulating paternal care because it reduces fear and hence enhances tolerance.

The ability to form social bonds, being those pair or parental bonds, may be influenced early during development in response to individual infant rearing styles or to extrinsic environmental variables (e.g., war, famine,

pathogenic load). This proposal implies the existence of a high degree of phenotypic plasticity, which is a salient feature of primate adaptation in general and human adaptation in particular (Quinlan 2007). The incorporation of, possibly adaptive, developmental programming into models of paternal care may help explain the intra- and interpopulation variation in the expression of paternal behaviors. Studies of paternal care provide an ideal model to understand the epigenesis of complex behavioral traits in model systems that are characterized in the field and the laboratory.

FUTURE ISSUES

1. From a life-history approach, the energetic costs of providing paternal care should be reflected in the life history of the species. How does paternal care affect the developmental trajectory of offspring?
2. Given the broad taxonomic distribution of paternal care, different evolutionary trajectories may have resulted in the same outcome. Titi and owl monkeys may be excellent models for studying homoplasy in paternal care.
3. Developmental programming and transgenerational effects are particularly exciting areas of future research on parental behavior. Biocultural models of developmental histories may explain the variation in the expression of paternal behavior in human societies. If so, what does this tell us about the evolution of the human family?
4. Given the flexibility in primate behavioral patterns, more data are needed on variation within and among populations. To identify successfully subtle differences among individuals in a population or among populations, data collection procedures need to be better validated across field sites, species, and researchers.
5. Genetic studies of paternity need to examine the costs and benefits of care at a community level to incorporate possible kin selection effects.

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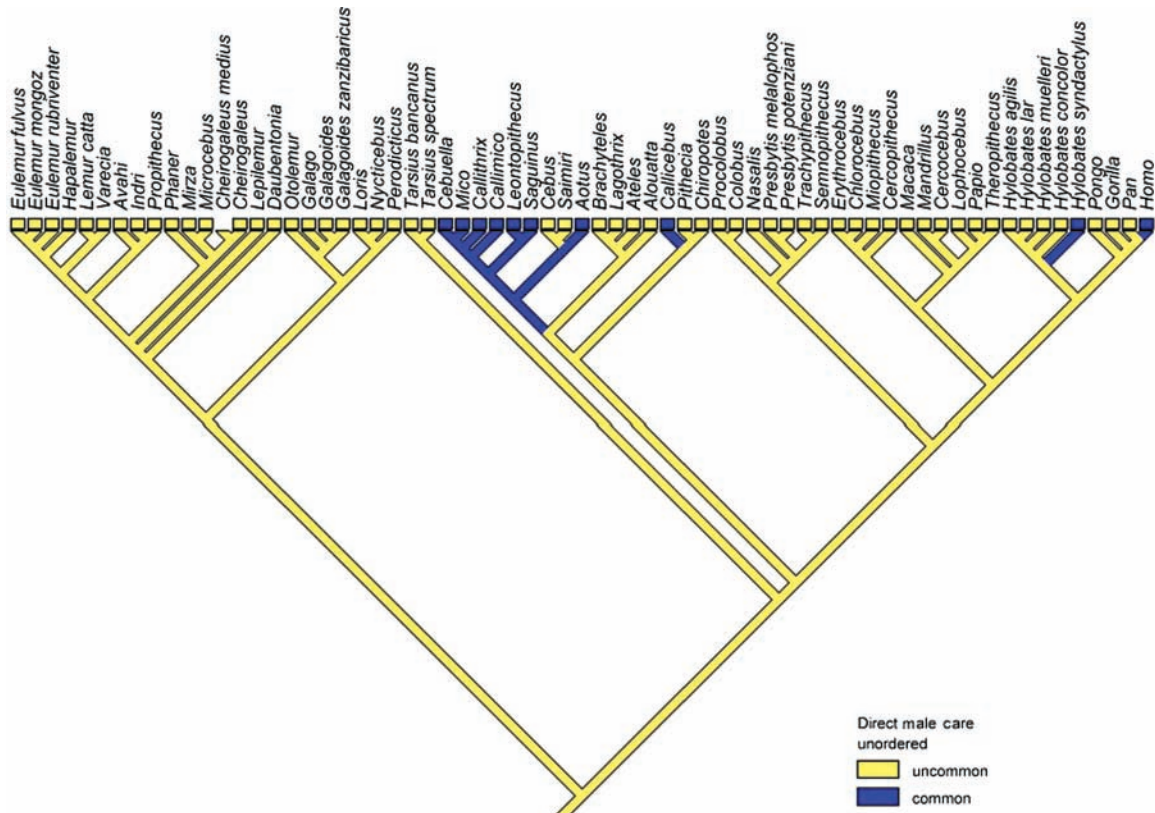


Figure 1

Primate phylogeny showing the taxa where paternal care is direct and conspicuous (*dark branches*).



Figure 2

A titi monkey infant (*Callicebus moloch*) sits in physical contact with his father.



Figure 3

An owl monkey infant (*Aotus azarae*) rides dorsally on the back of his father.



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Errata

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